
POLLINATION BIOLOGY
OF *LAPEIROUSIA* SUBGENUS
LAPEIROUSIA (IRIDACEAE)
IN SOUTHERN AFRICA;
FLORAL DIVERGENCE AND
ADAPTATION FOR
LONG-TONGUED
FLY POLLINATION¹

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ABSTRACT

Lapeirousia subg. *Lapeirousia* (Iridaceae) consists of 21 species endemic to sub-Saharan Africa, with the Mediterranean southwestern part of southern Africa the center of diversity. Analysis of the floral ecology of 19 species shows that the majority secrete large amounts of sucrose-rich or sucrose-dominant nectar, and the 16 species for which pollinator observations were obtained are cross-pollinated exclusively by insects with elongated mouth parts, representing three orders (Diptera, Hymenoptera, and Lepidoptera). In the absence of pollinators, at least four species (*L. arenicola*, *L. jacquinii*, *L. oreogena*, *L. simulans*) were found to set seed without cross pollination and are assumed to be mechanically autogamous. The 20 species segregate into three pollination types based on divergent patterns of pigmentation, scent production, perianth tube length, and pollinator taxa. Species with flowers of the *L. silenoides*-type are pollinated exclusively by *Prosoeca* species (Diptera: Nemestrinidae), and species with flowers of the *L. fabricii*-type are pollinated exclusively by *Moegistorhynchus longirostris* (Diptera: Nemestrinidae) and *Philoliche gulosa* (Diptera: Tabanidae). The latter two fly species, together with the *Prosoeca* species, have the longest mouth parts of all pollinators examined on species of subgenus *Lapeirousia*. The *L. divaricata*-type flower is pollinated by a combination of bees, mostly female Anthophoridae (e.g., *Anthophora*, *Amegilla*, *Tetraloniella*) and native *Apis mellifera* (Apidae), and to a lesser extent by bombyliid flies and some Lepidoptera. Observations of insect pollen load analysis suggest that the evolution of these three flower types has encouraged ethological isolation between species, but is a small component in broader pollination guilds encompassing co-blooming species in other genera and families, including Asteraceae, Geraniaceae, Scrophulariaceae, and Sterculiaceae. Mapping of pollination syndromes on a phylogenetic tree of subgenus *Lapeirousia* demonstrates the extreme adaptive radiation in the subgenus and the convergent development of the same pollination strategy repeatedly across the subgenus.

Africa is the center of diversity for the family Iridaceae, with the majority of species concentrated in the temperate and Mediterranean regions in the southern part of the continent (Goldblatt, 1978, 1994). One striking feature of the iridaceous flora of southern Africa is the variation in floral form and color (see Marloth, 1917–1932; Jeppe, 1989). By far the greater proportion of species of Iridaceae in southern Africa have flowers in which the perianth forms an elongated tube and the stamens and style are often prominently displayed. Although the te-

pals of such flowers do not have the characteristic shape found in *Iris* or *Moraea*, these tubular flowers exhibit a wide variety of colors, color patterns, and tepal orientation. The floral ecology of Iridaceae with exaggerated floral tubes has received less attention than those genera of the family with gullet blossoms (sensu Faegri & van der Pijl, 1979).

Within the southern African Iridaceae there are genera with more typical *Iris*-type flowers in which each flower is a meranthium. That is, each flower functions as three separate reproductive units, each

¹ Support for this study by grant 4816-92 from the National Geographic Society is gratefully acknowledged. We thank C. D. Michener and R. W. Brooks, Snow Entomological Museum, University of Kansas, for the anthophorid and megachilid bee identifications, and W. Whitehead, South African Museum, Cape Town, for the loan of *Parafidelia* bees seen foraging on *Lapeirousia barklyi*; B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for the nectar analyses; the South African Department of Environment Affairs and the Cape Department of Nature and Environmental Conservation for providing collecting permits; and Donna Stevens for the insect illustrations.

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consisting of a stamen and a stigma hidden between ornate style crests and a spreading tepal (e.g., *Moraea*, *Dietes*, *Gynandris*). Initial work on the floral ecology of *Moraea* (Vogel, 1954; Goldblatt et al., 1989) suggested that this genus has a pollination mechanism similar to those *Iris* species in the Northern Hemisphere (Faegri & van der Pijl, 1979) in which the pollination biology has been studied. Here heavy insects (usually bees and wasps) depress the drooping tepal to probe the floral interior for nectar and contact the sexual organs of the flower.

Most of the literature on the pollination ecology of tubular-flowered Iridaceae in southern Africa consists of little more than brief descriptions (Scott Elliot, 1890, 1891; Marloth, 1908, 1917–1932; Vogel, 1954; Johnson, 1992). This literature suggests that Iridaceae with tubular flowers may be pollinated by a wider variety of animals with much elongated mouth parts, including sunbirds, bees, flies in the families Nemestrinidae, Tabanidae, and Bombyliidae, sphinx moths, and other Lepidoptera, notably *Meneris tulbaghia* (Satyridae). Both the taxonomic literature and the brief reports of pollination observations indicate that tubular flowers specialized for pollination by these vectors have evolved in many families distributed through southern Africa, including the Amaryllidaceae, Crassulaceae, Ericaceae, Geraniaceae, Orchidaceae, Proteaceae, Scrophulariaceae, etc. (Vogel, 1954; Johnson, 1992; Johnson & Bond, 1994; Johnson et al., 1993).

Long-term fieldwork and quantitative analysis of the floral ecology of tubular-flowered Iridaceae has been confined so far to work on the genus *Nivenia* (Goldblatt & Bernhardt, 1990). Flowers in this genus are homostylous or heterostylous and are pollinated primarily by long-tongued flies in the genus *Prosoeca* (Nemestrinidae) and secondarily by female anthophorid bees. Is this pollination syndrome characteristic of other tubular-flowered Iridaceae in southern Africa?

Lapeirousia represents a far more promising genus for fieldwork on floral ecology of the African Iridaceae. This genus consists of 41 species in two subgenera, of which subgenus *Lapeirousia* has the more visibly diverse and specialized floral forms. Subgenus *Lapeirousia* is also easier to study, since many of its species have a narrowly circumscribed distribution, compared with the almost pan-sub-Saharan African subgenus *Paniculata* (Goldblatt, 1990). Nineteen of the 21 species in subgenus *Lapeirousia* occur along the west coast and near interior of southern Africa, and flowering sites for most species are easily accessible (Goldblatt, 1972; Goldblatt & Manning, 1994). The other two species, *L.*

littoralis Baker and *L. odoratissima* Baker, are widespread across south tropical Africa, and are thus outside our study area. To elucidate the dynamics of pollination in *Lapeirousia*, observations will be compared with results of the earlier study of *Nivenia* and with what is known about the pollination ecology of tubular flowers of southern Africa in general.

MATERIALS AND METHODS

Lapeirousia species grow in a variety of habitats ranging from montane areas to coastal flats, and in various soils, including coarse sands of various origins, shales and clays, and granites. Plants are often fairly common locally, but species have distribution patterns ranging from extremely local to widespread. Species of subgenus *Lapeirousia* include local endemics such as *L. verecunda* and *L. simulans*, both known from single extended populations in Namaqualand, and widespread species such as *L. anceps*, *L. fabricii*, and *L. pyramidalis*, that extend over half the entire southern African range of the subgenus. The species studied, study sites, and voucher information are listed in Table 1. Voucher specimens were made for all populations of *Lapeirousia* studied, also for species of other plant taxa observed to be visited by the same insect taxa collected on *Lapeirousia*. Plant vouchers are deposited at the Missouri Botanical Garden Herbarium, St. Louis (MO), and the Compton Herbarium, Cape Town (NBG).

Observation of insect foraging involved 4–20 hours per plant species from 1992 to 1994, and included aspects such as the frequency (number of visits per unit time) and taxonomic diversity of floral foragers, and how they removed rewards from flowers. When observed to probe the floral tube or contact the anthers or stigma, insects were captured and killed in a jar using ethyl acetate fumes. Location of pollen deposits was based on the examination of pinned insects. Pollen was removed from individual insects after pinning by placing the insect on a glass slide and gently rinsing the whole body in 100% ethanol while gently dislodging pollen loads on the frons, thorax, and in the case of bees, hind legs, with a dissecting needle. When the ethanol had evaporated the pollen residue was stained and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). To prevent contamination of the body of an insect with pollen carried by another in the same killing jar, the bodies of insect specimens were isolated from each other by wrapping them in tissue. The pollen of a plant species was scored as present on the body of an insect if

Table 1. Species of subgenus *Lapeirousia* studied, with voucher and study site information. All sites are in the Western Cape and Northern Cape Provinces, South Africa; voucher specimens are located at MO and NBG. Asterisks (*) mark main study site and source of nectar sugar data in Tables 3 and 4 where there is more than one study site.

Species	Study site and voucher information
<i>L. anceps</i> (L.f.) Ker-Gawl.	Near Ysterfontein, N of Cape Town, <i>Manning s.n.</i> (no voucher)*; Olifants River Valley, 15 km N of Clanwilliam, <i>Goldblatt & Manning 9697</i> (no voucher)
<i>L. arenicola</i> Schltr.	Knersvlakte, 10 km N of Vanrhynsdorp, <i>Goldblatt & Manning 9453</i>
<i>L. exilis</i> Goldblatt	Ratelpoort, N of Springbok, <i>Goldblatt & Manning 9897</i>
<i>L. barklyi</i> Bak.	Richtersveld, dunes W of Grasvlakte, <i>Goldblatt & Manning 9460</i>
<i>L. dolomitica</i> Dinter subsp. <i>dolomitica</i>	Richtersveld, hills above farm Grasvlakte, <i>Goldblatt & Manning 9308</i>
subsp. <i>lewisiana</i> B. Nord.	Namaqualand, 10 km S of Garies, <i>Goldblatt & Manning 9188</i>
<i>L. divaricata</i> N. E. Br.	Bidouw Valley, alluvium at foot of pass, <i>Goldblatt 9190*</i> ; valley bottom between Doornbosch and Bidouw, <i>Goldblatt & Manning 9633</i>
<i>L. fabricii</i> (Delaroche) Ker-Gawl.	Top of Spektakel Pass, W of Springbok, <i>Goldblatt & Manning 9711*</i> ; Olifants River Valley, near Citrusdal, <i>Goldblatt & Manning 10030</i>
<i>L. jacquinii</i> N. E. Br.	Farm Driefontein, S of Nieuwoudtville, <i>Goldblatt & Manning 9412*</i> ; Top of Botterkloof Pass, <i>Goldblatt & Manning 9966</i>
<i>L. macrospatha</i> Bak.	Richtersveld, farm Grasvlakte, sandy plain, <i>Goldblatt & Manning 9455</i>
<i>L. montana</i> Klatt	Klein Roggeveld, foot of Komsberg Pass, <i>Goldblatt & Manning 9672C</i>
<i>L. oreogena</i> Schltr. ex Goldblatt	Glen!yon farm, Nieuwoudtville, <i>Goldblatt & Manning 9643A</i>
<i>L. plicata</i> (Jacq.) Diels	Flats below the Hantamsberg, Calvinia, <i>Goldblatt & Manning 9912</i>
<i>L. pyramidalis</i> (Lam.) Goldblatt subsp. <i>pyramidalis</i>	Hill W of Worcester, <i>Goldblatt & Manning 9592*</i> ; mountain slopes E of De Wet, <i>Goldblatt & Manning s.n.</i> (no voucher); foot of Hex River Pass, <i>Goldblatt & Manning 9435A</i>
subsp. <i>regalis</i> Goldblatt & Manning	Olifants River Valley opposite Trawal, <i>Goldblatt & Manning 9909*</i> ; Olifants River Valley near Klawervlei, <i>Goldblatt & Manning 9223</i>
<i>L. silenoides</i> (Jacq.). Ker-Gawl.	Namaqualand, between Garies and Kamieskroon, <i>Goldblatt & Manning 9467*</i> ; Spektakel Pass, W of Springbok, <i>Goldblatt & Manning 9327</i>
<i>L. simulans</i> Goldblatt & Manning	Knersvlakte, 10 km N of Vanrhynsdorp, <i>Goldblatt & Manning 9454</i>
<i>L. spinosa</i> (Goldblatt) Goldblatt & Manning	Richtersveld, near farm Grasvlakte, <i>Goldblatt & Manning 9456</i>
<i>L. tenuis</i> (Goldblatt) Goldblatt & Manning	Plains 62 km W of Springbok to Grootmis, <i>Goldblatt & Manning 9935</i>
<i>L. verecunda</i> Goldblatt	E slopes of Spektakel Pass, <i>Goldblatt & Manning 9144</i>
<i>L. violacea</i> Goldblatt	Top of Botterkloof Pass, <i>Middlemost 1605</i>

more than 10 individual grains (or polyads) were counted on the slide (Table 2).

Field estimates of nectar volume were made from unbagged flowers, thus nectar volumes (Table 4) represent the result of secretion and exploitation. To extract nectar, flowers were picked and nectar was withdrawn from the base of the floral tube with 3- μ l capillary tubes after separating the ovary from the perianth. Nectar samples were dried on Whatmans filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for analysis (Table 3). The percentage of sugars dissolved in fresh nectar (Table 4) was recorded on a Bellingham & Stanley hand-held refractometer (0–50%) using nectar extracted from flowers in the manner described above. Most nectar sugars were analyzed in the field, but a few samples were taken from flowers of cut stems placed in water. Flowers of *Lapeirousia* last well in water, and the chemistry of nectar sugars was evidently not affected by the

latter treatment, but nectar volumes were found to be higher than in specimens examined in the field, presumably because visitors were excluded, and water availability was not limiting.

Identification of all insects collected (Tables 2, 5), excluding bees, was made by comparing our specimens with existing collections. Bee identifications except for *Apis*, *Parafidelia*, and *Tetraloniella* (provided by V. Whitehead, South African Museum, Cape Town) were made by C. D. Michener and R. W. Brooks, Snow Entomological Museum, Lawrence, Kansas. Insect voucher specimens are housed at the Snow Entomological Museum, Lawrence, Kansas, and the Natal Museum, Pietermaritzburg, South Africa.

RESULTS

INFLORESCENCE ARCHITECTURE

Most species of subgenus *Lapeirousia* have a simple or branched flowering stem, and each axis

Table 2. Analyses of pollen loads carried by insects collected on *Lapeirousia* species. *Prosoeca* = *Pr.*; *Tetraloniella* = *T.*; *Megistorhynchus* = *M.*; *Philoliche* = *Ph.*; *Parafidelia* = *Pa*; *Anthophora* = *A.*; *Heliotis* = *H.* Pollen types abbreviated as follows: *Ac* = *Acacia*; *An* = *Anthericaceae*; *Co* = *Asteraceae*; *Gr* = *Grielum*; *He* = *Hermannia*; *La* = *Lapeirousia*; *Op* = orchid pollinium; *Pa* = papilionoid legume (?*Wiborgia*); *Pe* = *Pelargonium*; *Po* = *Polygala*; *Sc* = *Scrophulariaceae*; *Wa* = mixed campanulales (?*Wahlenbergia*, *Prismatocarpus*); *Ud* = unidentified dicot; *Um* = unidentified monocot. Figures in parentheses after insect names indicate number of individuals. Figures in columns 3–16 are the numbers of insects bearing a particular pollen type.

<i>Lapeirousia</i> species		Insect taxon (n)	Pollen loads													
			Ac	An	Co	Gr	He	La	Op	Pa	Pe	Po	Sc	Wa	Ud	Um
Subgenus <i>Lapeirousia</i>																
<i>L. silenoides</i> group																
<i>L. dolomitica</i>	Diptera															
	<i>Pr. peringueyi</i> (1)	—	—	—	—	—		1	—	—	—	—	—	—	1	—
<i>L. jacquinii</i>	Diptera															
	<i>Pr. sp.</i> (2)	—	—	—	—	—		2	—	—	—	—	—	1	1	1
	<i>Pr. peringueyi</i> (3)	—	—	—	—	—		3	—	2	—	—	—	—	—	—
<i>L. oreogena</i>	Diptera															
	<i>Pr. sp.</i> (5)	—	—	3	—	—		5	—	—	—	—	—	—	—	—
<i>L. pyramidalis</i>	Diptera															
subsp. <i>regalis</i>	<i>Pr. peringueyi</i> (5)	—	—	—	—	—		5	—	—	—	—	—	—	—	—
<i>L. silenoides</i>	Diptera															
	<i>Pr. peringueyi</i> (9)	—	—	—	—	—		9	—	—	8	—	—	—	—	1
<i>L. violacea</i>	Diptera															
	<i>Pr. peringueyi</i> (2)	—	—	1	—	—		2	—	—	—	—	—	—	—	—
<i>L. divaricata</i> group																
<i>L. barklyi</i>	Hymenoptera															
	<i>Pa. major</i> (1)	1	1	1	1	—		—	—	—	—	—	—	—	—	—
<i>L. exilis</i>	Diptera															
	Bombyliid (2)	—	—	—	—	—		2	—	—	—	—	—	—	—	—
	Hymenoptera															
	<i>Apis mellifera</i> (5)	—	—	—	—	—		5	—	—	—	—	—	—	—	—
<i>L. divaricata</i>	Lepidoptera															
	<i>H. armigera</i> (2)	—	—	2	—	—		1	—	—	—	1	—	—	—	—
	Hymenoptera															
	<i>A. diversipes</i> (5)	—	—	4	—	1		5	—	1	2	—	—	1	2	1
	<i>A. krugeri</i> (2)	—	—	1	—	2		2	—	—	1	—	—	—	—	—
	<i>A. schulzei</i> (1)	—	—	1	—	—		1	1	—	—	—	—	—	—	—
	<i>A. braunsii</i> (1)	—	—	—	—	1		1	—	—	—	—	—	—	—	—
	<i>Amegilla grisella</i> (1)	—	—	—	—	1		1	—	—	—	—	—	—	—	—
<i>L. montana</i>	Diptera															
	Bombyliid (2)	—	—	1	—	—		2	—	—	—	—	—	—	—	—
	Hymenoptera															
	<i>A. krugeri</i> (1)	—	—	1	—	1		1	—	—	—	—	—	—	—	—
	Lepidoptera															
	<i>Cynthia cardui</i> (1)	—	—	1	—	—		1	—	—	—	1	—	—	1	—
	<i>H. armigera</i> (2)	—	—	1	—	—		—	—	—	—	—	—	—	—	—
<i>L. plicata</i>	Hymenoptera															
	<i>Apis mellifera</i> (6)	—	—	—	—	—		6	—	—	—	—	—	—	—	—
	<i>T. cf. karroica</i> (4)	—	—	—	—	—		4	—	—	—	—	—	—	—	—
<i>L. spinosa</i>	Hymenoptera															
	<i>Hoplitis similis</i> (1)	—	—	1	—	—		1	—	—	—	—	—	—	—	—
<i>L. fabricii</i> group																
<i>L. anceps</i>	Diptera															
	<i>M. longirostris</i> (1)	—	—	1	—	—		1	—	—	1	—	—	1	1	—
<i>L. fabricii</i>	Diptera															
	<i>Ph. gulosa</i> (4)	—	1	1	—	—		4	—	—	2	1	—	—	1	—
	<i>M. longirostris</i> (3)	1	1	2	—	—		3	1	—	—	—	1	—	2	—

Table 2. Continued.

<i>Lapeirousia</i> species	Insect taxon (n)	Pollen loads													
		Ac	An	Co	Gr	He	La	Op	Pa	Pe	Po	Sc	Wa	Ud	Um
Subgenus <i>Paniculata</i>															
<i>L. azurea</i>	Hymenoptera														
	<i>A. diversipes</i> (2)	—	—	2	—	1	2	1	—	1	—	—	1	2	1
<i>L. fastigiata</i>	Hymenoptera														
	<i>A. diversipes</i> (1)	1	—	—	—	—	1	—	—	—	—	—	—	1	—
	<i>Hoplitis similis</i> (1)	—	—	1	—	—	1	—	—	1	—	—	—	—	—
<i>L. neglecta</i>	Hymenoptera														
	<i>Xylocopa hottentotta</i> (1)	—	—	1	—	—	1	—	—	—	—	—	—	1	—

terminates in a spike of several to many flowers. In *L. oreogena*, *L. montana*, *L. plicata*, and *L. odoratissima* the inflorescence is a congested tuft of flowers borne at ground level. The number of flowers per plant varies considerably from year to year. Vigorous plants have as many as five spikes each and up to 20 flowers per tuft or spike.

FLORAL PHENOLOGY AND LIFE SPAN

Flowering in southern African species of subgenus *Lapeirousia* in the study area ranges from late May until early November (Fig. 1). Populations of each species bloom for two to four weeks. Exact timing of flowering within a species varies seasonally, and to some extent locally, depending on elevation and aspect. The higher the elevation the later a population comes into bloom. Despite considerable overlap in flowering times (Fig. 1), species may be characterized generally as early (June to mid August), mid (late August and September), or late season (October and November) bloomers.

The pattern of flower buds opening on an inflorescence is acropetal. In all species the perianth of a mature bud expands in the early to mid morning. The rate at which buds open and the longevity of the expanded perianth are dependent on ambient temperatures. The perianth of an open flower lives a maximum of five days if daily temperatures remain below 20°C and soils remain wet. At sunset the tepals of most species contract, partly or sometimes completely enclosing the exerted anthers and stigmas. In *L. exilis*, tropical African *L. odoratissima*, and *L. pyramidalis* (both subspecies) the tepals remain open all night.

The anthers of all species dehisce longitudinally within two to four hours after the tepals unfold. Pollen remains in the open thecae until contacted by insects or washed out by rain. The three styler lobes do not normally expand to expose the receptive

stigmas until the day after the anthers have dehisced. This suggests that all the species studied are weakly protandrous.

FLORAL MORPHOLOGY (FIG. 2)

In most species of subgenus *Lapeirousia* the perianth tube is cylindric. In *L. divaricata* and *L. spinosa*, however, the tube is funnel-shaped (Fig. 2H). In sixteen species the perianth tube always exceeds 17 mm in length, with a maximum of 76 mm in *L. anceps* (Table 5). In *L. divaricata*, *L. spinosa*, and *L. tenuis* the tube is less than 16 mm long. In *L. exilis*, *L. montana*, and *L. plicata*, however, the external length of the tube is misleading: the lower half of the tube is occluded by the style and intrusive ridges, decurrent on the filaments (Fig. 2K), so that the nectar is forced into the upper part of the tube. Functional tube length, in terms of accessibility of nectar to insects, is less than half what it appears to be (Table 5). Tube length is unusually variable in *L. anceps*, and may be as little as 20–30 mm in populations in the south of its range, and 45–76 mm in the west and north.

Seventeen species have a zygomorphic flower and unilateral, arcuate stamens and style (Table 5, Fig. 2A, E, H). In contrast, *L. oreogena*, *L. montana*, *L. plicata*, and *L. odoratissima* have actinomorphic flowers (Fig. 2J, K) in which the stamens and style are symmetrically disposed.

Tepals of the fully open flower either spread horizontally and are thus patent, or the dorsal (adaxial) tepal is erect (*Lapeirousia silenoides*, *L. pyramidalis*, *L. verecunda*), or inclined over the stamens (*L. divaricata*, *L. spinosa*). In species with zygomorphic flowers the dorsal tepal is broader and sometimes longer than the five other tepals. *Lapeirousia fabrii* and *L. barklyi* are the only species in which the tepals are broadly cupped below and patent above, and thus include the filaments. In several species with zygomorphic flowers (e.g., *L. divaricata*, *L. fa-*

Table 3. Nectar sugars in subgenus *Lapeirousia*. Nectar analyses for subgenus *Lapeirousia* were provided by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, South Africa. Taxa of subgenus *Lapeirousia* are grouped according to flower type and pollinator class as in Table 2.

Species	Sample size n	Range of sugars %			Sucrose/ (Fru + Glu)
		Fru	Glu	Suc	
<i>L. silenoides</i> group					
<i>L. dolomitica</i>					
subsp. <i>dolomitica</i>	2	4–9	12–14	77–84	3.35–5.25
subsp. <i>lewisiana</i>	4	5–8	14–19	74–81	2.85–4.26
	1	12	25	63	1.7
<i>L. jacquinii</i>	1	8	17	75	3.00
<i>L. oreogena</i>	4	11–17	19–25	58–69	1.38–2.26
<i>L. pyramidalis</i>					
subsp. <i>regalis</i>	3	8–12	14–17	74–81	2.45–3.55
	3	4–21	12–36	48–84	0.92–5.25
<i>L. silenoides</i>	3	5–8	18–27	65–77	1.86–3.35
<i>L. violacea</i>	1	9–13	15–16	71–76	2.45–3.17
<i>L. divaricata</i> group					
<i>L. barklyi</i>	1	36	40	24	0.32
<i>L. divaricata</i>	1	18	28	54	1.17
<i>L. exilis</i>	3	11–16	19–25	59–70	1.44–2.33
<i>L. montana</i>	3	6–24	16–30	46–88	0.85–4.00
<i>L. plicata</i>	2	15–16	21–31	54–63	1.17–1.70
<i>L. pyramidalis</i>					
subsp. <i>pyramidalis</i>	4	5–11	12–22	71–73	2.45–4.88
<i>L. spinosa</i>	1	13	20	67	2.03
<i>L. fabricii</i> group					
<i>L. anceps</i>	3	6–20	20–26	54–74	1.17–2.85
<i>L. arenicola</i>	4	5–11	10–18	71–85	2.45–5.67
<i>L. fabricii</i>	4	12–21	21–26	53–67	1.13–2.03
<i>L. macrospatha</i>	1	34	43	23	0.29
<i>L. simulans</i>	1	18	23	59	1.44
<i>L. verecunda</i>	2	8	18	74	2.85

bricii—Fig. 2H), each of the three lower tepals bears a raised ridge or narrow tooth. These appendages are absent in species with actinomorphic flowers.

In all species the stamens are equal in size, and the filaments are erect or sometimes slightly inclined. In zygomorphic-flowered species the anthers are parallel and face the center of the flower and the lower tepals and nectar guides, but in species with actinomorphic flowers the anthers are symmetrically disposed and face outward (Fig. 2J, K). The style branches of all species of subgenus *Lapeirousia* included in the study are divided for half their length. Although this is a generic characteristic, the style branches may be undivided in some species or populations of the genus (Goldblatt, 1972, 1990). The resulting six styler arms, which spread outward and recurve, bear receptive stigmatic hairs that appear to be dry when observed

under a 10× hand lens. The style arms are normally held between 1 and 3 mm above the anther apices, but in *L. arenicola*, *L. jacquinii*, *L. simulans*, and *L. violacea* the style arms become tangled in the anthers as the style lobes expand.

COMPATIBILITY AND FRUIT SET

We were unable to make a thorough study of compatibility in subgenus *Lapeirousia* but present the following observations. In *L. arenicola*, *L. jacquinii*, *L. simulans*, and *L. violacea*, stems cut at bud stage, maintained in water, and excluded from insects for two weeks routinely set full capsules containing the normal number of seeds for that species. Furthermore, *L. jacquinii* and *L. oreogena* have been noted to set seed in greenhouses where insect activity was excluded.

Lapeirousia barklyi, *L. dolomitica* subsp. *dolomi-*

Table 4. Nectar concentration and volume in subgenus *Lapeirousia*. Taxa of subgenus *Lapeirousia* are grouped according to flower type and pollinator class as in Table 2. Figures for nectar sugar concentration are means, standard deviation given in parentheses, but ranges are provided for less than three observations.

Species	Sample size	Nectar conc. (%)	Nectar volume (ml)
<i>L. silenoides</i> group			
<i>L. dolomitica</i>			
subsp. <i>dolomitica</i>	5	30.4 (2.4)	1.4–3.1
subsp. <i>lewisiana</i>	4	27.0 (0.8)	5.1–5.5
<i>L. jacquinii</i>	5	27.3 (2.9)	1.5–2.3
	1	25	1.5
<i>L. oreogena</i>	10	25.8 (1.6)	2.5–7.3
<i>L. pyramidalis</i> subsp. <i>regalis</i>	10	28.4 (2.8)	2.6–4.8
	3	28.2 (0.8)	2.6–4.8
<i>L. silenoides</i>	10	26.5 (1.1)	1.7–2.8
	3	29.0 (2.0)	2.3–3.6
	2	22–25	2.6–2.8
	1	26	2.1
<i>L. violacea</i>	3	25.0 (0)	1.5–1.6
	7	28.2 (2.9)	1.4–1.8
<i>L. divaricata</i> group			
<i>L. barklyi</i>	2	26–27.5	0.9–1.3
<i>L. divaricata</i>	7	26.7 (1.5)	0.6
<i>L. exilis</i>	10	34.1 (1.8)	0.9–1.7
<i>L. montana</i>	10	24.8 (2.2)	2.6–8.1
<i>L. plicata</i>	3	28.3 (3.2)	0.9–1.7
<i>L. pyramidalis</i> subsp. <i>pyramidalis</i>	3	30.1 (4.9)	0.7–1.7
	7	34.1 (1.6)	0.8–3.0
<i>L. spinosa</i>	2	31–32	1.1–1.2
<i>L. tenuis</i>	6	46.1 (5.1)	0.4–1.0
<i>L. fabricii</i> group			
<i>L. anceps</i>	10	23.5 (1.3)	1.5–3.1
	7	21.1 (1.4)	1.4–3.2
<i>L. arenicola</i>	4	32.8 (2.1)	0.6–0.7
<i>L. fabricii</i>	10	32.5 (2.3)	1.3–3.4
	5	24.8 (2.6)	0.8–1.5
	7	25.2 (1.1)	0.4–0.9
<i>L. macrospatha</i>	10	23.8 (1.5)	0.7–3.3
	3	21.0 (1.0)	3.5–5.7
<i>L. simulans</i>	4	25.8 (1.7)	0.8–1.5
<i>L. verecunda</i>	10	26.6 (2.5)	0.6–3.0

tica, *L. pyramidalis*, *L. silenoides*, and *L. spinosa* did not set fruit when inflorescences were maintained in water as in the species above. In these taxa dehisced anthers and stigmatic surfaces are in contact in both field populations and laboratory specimens. *Lapeirousia silenoides* and *L. pyramidalis* subsp. *regalis*, in which the anthers and stigmas are not in contact, do not set fruit even when self-pollinated by hand whether maintained in water or grown in pots. In field populations of *L. dolomitica*, *L. pyramidalis*, and *L. silenoides* individual plants were often observed to produce none, or only one or two mature capsules per spike after flowering.

FLORAL PRESENTATION, ATTRACTANTS, AND REWARDS

Field observations of species of subgenus *Lapeirousia* indicate that they can be divided into three morphological types based on floral characteristics (Tables 3, 4, 5), and that each of the floral types is associated with a different suite of pollinators. The three flower types are defined primarily by floral pigmentation and patterning in combination with perianth tube length. However, regardless of flower type, in zygomorphic flowers visible nectar guides are always confined to the three lower tepals (Fig.

Table 5. Floral characters and pollinators of *Lapeirousia* subg. *Lapeirousia* of Namaqualand and the Cape West Coast. *Prosoeca* and *Megistorhynchus* are long-proboscid flies of the family Nemestrinidae; *Philoliche* is a long-tongued fly of the family Tabanidae (only *P. gulosa* has been collected on species of subgenus *Lapeirousia*). Data here represent original observations; pollination of *L. oreogena* by *Prosoeca* sp. was first observed by K. Steiner (pers. comm.); pollination of *L. anceps* by *M. longirostris* was first reported by Hesse in Vogel (1954). Visits to *L. barklyi* by *Parafidelia major*, its presumed pollinator, have been noted by V. Whitehead (pers. comm.). Z = zygomorphic; A = actinomorphic; V = vivid red, purple, or violet shades with contrasting pale nectar guides; P = pale blue (or pink); W = white; CR = pale cream with red markings; N = no scent; S = weak odor; SS strong odor; — = no data.

Species	Flower			Pollinator	Mouth part mm	Floral tube mm
	Sym- metry	Color	Scent			
<i>L. silenoides</i> group						
<i>L. dolomitica</i>						
subsp. <i>dolomitica</i>	Z	V	S	<i>Prosoeca peringueyi</i>	33	35–40
subsp. <i>lewisiana</i>	Z	V	N	—	—	45–50
<i>L. jacquinii</i>	Z	V	N	<i>Pr. sp.</i> and <i>Pr. peringueyi</i>	30	33–35
<i>L. pyramidalis</i> subsp. <i>regalis</i>	Z	V	N	<i>Pr. peringueyi</i>	35	40–47
<i>L. oreogena</i>	A	V	N	<i>Pr. sp.</i>	37	53–63(–70)
<i>L. silenoides</i>	Z	V	N	<i>Pr. peringueyi</i>	35	43–55
<i>L. violacea</i>	Z	V	N	<i>Pr. peringueyi</i>	32	34–40
<i>L. divaricata</i> group						
<i>L. barklyi</i>	Z	P	N	Parafidelia	—	
<i>L. divaricata</i>	Z	W	S	noctuid moth and anthophorid bees	7–8 8–10	23–25 9–11
<i>L. exilis</i>	A	W	SS	bombyliid flies and honey bees	6–8	20–25 ¹
<i>L. montana</i>	A	P–W	S	various ²	6–12	43–55 ³
<i>L. plicata</i>	A	W	N	bombyliid flies and honey bees	6–8	15–20 ³
<i>L. pyramidalis</i> subsp. <i>pyramidalis</i>	Z	P	SS	hawkmoth	22	25–28
<i>L. spinosa</i>	Z	W	S	<i>Hoplitis similis</i>	5	10–12
<i>L. tenuis</i>	Z	P	S	—	—	12–15
<i>L. fabricii</i> group						
<i>L. anceps</i>	Z	CR	N	<i>Megistorhynchus</i>	54–60	65–76
<i>L. arenicola</i>	Z	CR	N	—	—	17–21
<i>L. fabricii</i>	Z	CR	N	<i>Megitorhynchus</i> and <i>Philoliche</i>	42–46 31–34	38–47 45–48
<i>L. macrospatha</i>	Z	CR	N	—	—	31–34
<i>L. simulans</i>	Z	CR	N	—	—	28–35
<i>L. verecunda</i>	Z	CR	N	—	—	38–49

¹ A pocket of air in the base of the tube forces the nectar upwards ca. 8–10 mm, effective tube length 8–10 mm.
² Anthophorid bees (*Anthophora krugeri*), butterflies (*Cynthia cardui*), bombyliid flies, noctuid moths.
³ Lower half of tube completely closed, effective tube length ca. 25 mm for *L. montana*, 5–8 mm for *L. plicata*.

2). In all species nectar is secreted at the base of the floral tube in volumes ranging from 20 to 76 ml (only 10–12 ml in *L. divaricata* and *L. spinosa*) (Table 4). In *L. exilis*, *L. montana*, and *L. plicata* occlusion of the basal part of the tube results in the nectar being forced into the upper half.

1. The *L. silenoides*-type (Fig. 2A): tepal pigmentation dark blue to purple or dark red, darker than the nectar guides; visible nectar guides yellow to white streaks or blotches near the tepal bases and sometimes a zone of intense pigmentation in the center of each lower tepal; callus ridges absent; no scent discernable to the human nose except in *L. dolomitica* subsp. *dolomitica*, which has a faint sweet odor; floral tubes 33–70 mm long; flowers actinomorphic or zygomorphic; nectar sucrose rich to sucrose dominant.

2. The *L. fabricii*-type (Fig. 2E): tepal pigmentation white to cream or pale pink (but usually pink to red on the reverse), lighter than the nectar guides; visible nectar guides dark red to maroon oblong to acute patterns at the tepal bases; callus

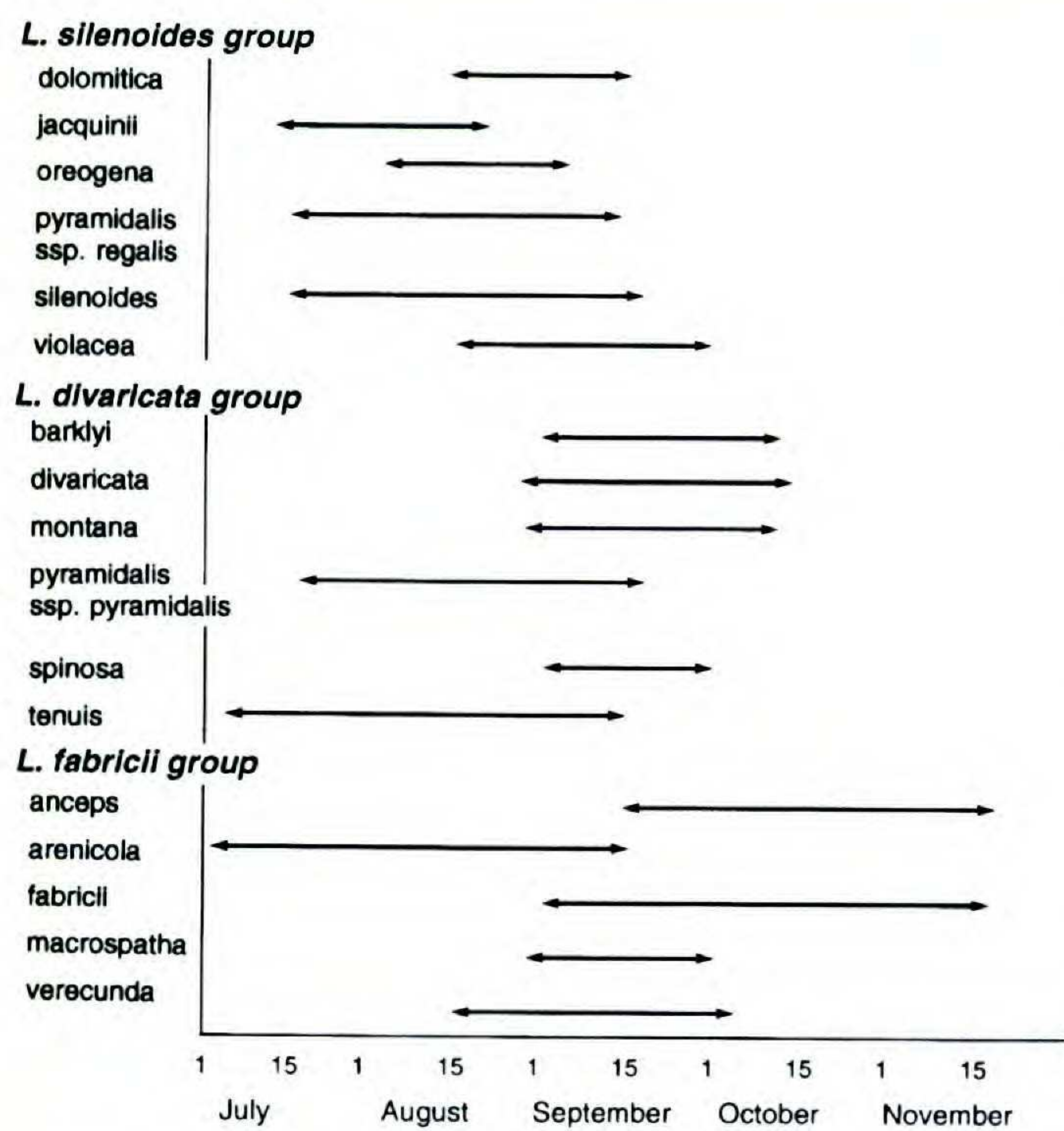


FIGURE 1. Flowering phenology of southern African species of subgenus *Lapeirousia* (i.e., excluding *L. odoratissima* and *L. littoralis* subsp. *caudata*). Species are arranged alphabetically in their respective floral guilds (Tables 2–5).

ridges usually present; no scent discernable to the human nose; floral tubes normally 30–76 mm long; flowers zygomorphic; nectar sucrose dominant or, in *L. macrospatha*, hexose rich.

3. The *L. divaricata*-type (Fig. 2H): tepal pigmentation white to cream or pale blue, lilac, or pink; visible nectar guides usually narrow to streaky, light purple sometimes grading to a yellow to cream-colored ridge at the base of the tepals or merely a white zone in the center of the flower (*L. montana*); scents present and variable, ranging from a cloyingly sweet heavy fragrance (*L. exilis*, *L. pyramidalis* subsp. *pyramidalis*) to a lightly sweet to mildly spicy scent reminiscent of *Dianthus* or *Narcissus*; callus ridges well developed in *L. divaricata*, *L. spinosa*, rare and inconspicuous in *L. pyramidalis* subsp. *pyramidalis*; floral tubes never exceeding 55 mm, in 3 of the 5 species tubes less than 30 mm (functional tube length always less than 35 mm); flowers actinomorphic or zygomorphic; nectar usually sucrose dominant, or sucrose rich (*L. montana*), or hexose rich (*L. barklyi*).

POLLINATION MECHANISMS

The three modes of floral presentation are accompanied by three different pollinator guilds. However, all floral foragers collected on *Lapeirousia* species had two foraging characters in common. First, pollen load analysis (Table 2) and observations of flight patterns indicate that all insects ob-

served on *Lapeirousia* (Figs. 2, 3) forage actively on the flowers of some other co-blooming plants (Table 2). Second, no matter how elongated the mouth parts of the pollinator are, they are always somewhat shorter than the perianth tube (Table 5). In addition, an insect was rarely observed to probe anthers with its proboscis or actively collect pollen on any *Lapeirousia* species.

1. The *Lapeirousia silenoides* group. Nectar foraging in this flower type was dominated by long-tongued flies of the genus *Prosoeca* (Nemestrinidae) (Figs. 3A, B, 4A). *Prosoeca peringueyi* was observed foraging on the flowers of all species in this group (Tables 2, 5) excluding *L. oreogena*. *Lapeirousia oreogena* was visited by *Prosoeca* sp. nov. (Fig. 3B), and this fly species also visited *L. jacquinii* at two sites on the Nieuwoudtville Plateau (where *P. peringueyi* evidently does not occur). In both species of flies the insects hover while orienting and inserting their proboscis into the tube. When the proboscis has been fully inserted into a tube that is long enough to permit this, the insect grasps the tepals with its legs during the actual feeding process, but the wings remain in motion. By flexing the tibiae of the hind legs forward, the fly can use all three pairs of legs for grasping, and this is done in plants with both vertical and horizontal flower presentation. In flowers with short tubes that are visited for nectar, the body does not contact the stamens or stigmas so that pollination is not effected, and the fly hovers without grasping the tepals.

Prosoeca species are active on mild to warm days from mid morning to early afternoon, and again in the late afternoon. These flies remain at each *Lapeirousia* flower for 3–5 seconds, and pollen adheres to the frons and thorax in *L. oreogena* and on the dorsum and upper frons in other species. Often pollen depositions are so heavy they are visible to the naked eye. In species with zygomorphic flowers, the fly always orients itself in the same way, approaching the flower from the front, thus facing the anthers as it forages. Density of visitors varies considerably, ranging from four to five flies present locally at the same time, to as few as one or two flies at sites over periods as long as an hour. At one site, the top of Botterkloof Pass, where *L. jacquinii* and *L. violacea* co-occur, individuals of *P. peringueyi* were observed to visit both species indiscriminately. *Prosoeca* species typically interrupted foraging on *Lapeirousia* species to collect nectar on other species growing nearby, including *Pelargonium* species (Geraniaceae), and taxa of Iridaceae including *Babiana* species, *Sparaxis variegata* subsp. *metelerkampiae* (L. Bolus) Goldblatt, *Xenoscapa uliginosa* Goldblatt & Man-

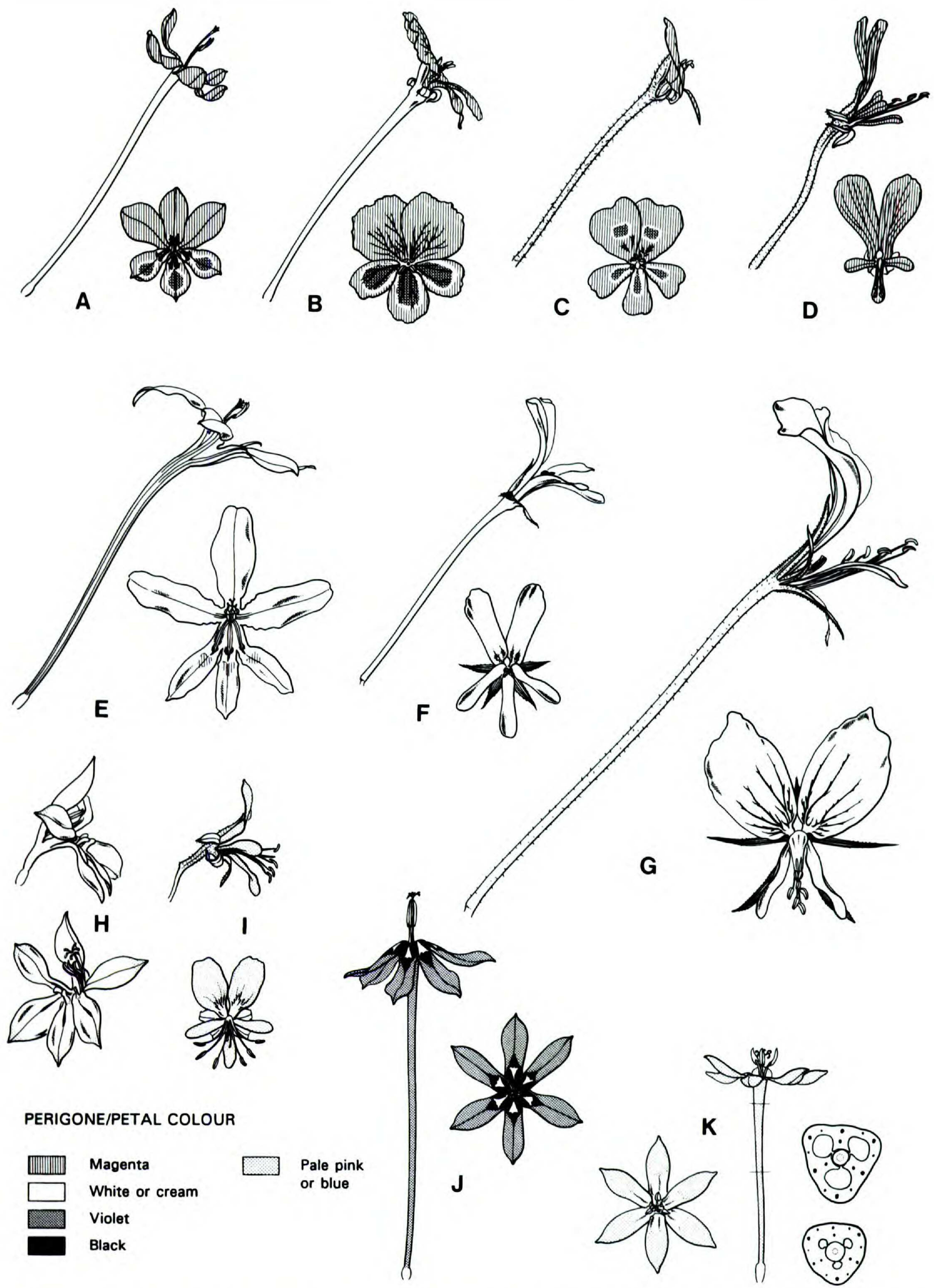


FIGURE 2. The main flower types in subgenus *Lapeirousia*, and selected flowers of other families resembling these flower types, which are visited by the same insects that are the primary pollinators of *Lapeirousia* species.—A. *L. silenoides*.—B. *Pelargonium sericifolium*.—C. *P. magenteum* J. J. A. Van der Walt.—D. *P. incrassatum* (Andr.) Sims.—E. *L. fabricii*.—F. *Pelargonium zonale* (L.) L'Hér. ex Sol.—G. *P. longicaule* (Jacq.) Harv.—H. *L. divaricata* (note prominent toothlike ridges on the lower tepals).—I. *Pelargonium scabrum* (L.) L'Herit.—J. *L. oreogena*.—K. *L. montana* (with transverse sections of the tube at different levels). Approximately $\times \frac{2}{3}$.



FIGURE 3.—A. *Prosoeca peringueyi* foraging on *Lapeirousia pyramidalis* subsp. *regalis*.—B. *Prosoeca* sp. nov. inserting its proboscis into the perianth tube of *L. oreogena*.—C. *Apis mellifera* foraging on *L. plicata*.—D. The noctuid moth *Heliotis armigera* grasping a flower of *L. divaricata*. Photographs were taken at study sites listed in Table 1.

ning, *Hesperantha latifolia* (Klatt) de Vos, and *Geissorhiza kamiesmontana* Goldblatt. Interestingly, the flowers of *Pelargonium sericifolium* van der Walt do not secrete nectar, although they have long floral tubes and may mimic flowers of species that do produce nectar (Fig. 2), suggesting pollination by deceit, a phenomenon best known in Orchidaceae.

Pollen deposition tends to be on the head and back part of the thorax (nototribic) in *Lapeirousia* except *L. oreogena*, but on the underside (sternotribic) in *Pelargonium*, a factor that reduces contamination of pollen loads and competition for vector sites on the insects' bodies.

2. The *L. fabricii* group. Nectar foraging in this group was limited to one species of fly in the Nemestrinidae (*Moegistorhynchus longirostris*—Fig. 4B) and one species of fly of the family Tabanidae (*Philoliche gulosa*—Fig. 4C). Both fly taxa are long-tongued and have mouth parts as long as or longer than the *Prosoeca* species discussed above. *Moegistorhynchus longirostris* was observed actively foraging on *L. fabricii* only in the late afternoon, 4:00–6:00 PM, at one study site in northern Namaqualand. The same fly species was recorded visiting *L. anceps* at the study site near Ysterfontein during the late morning on a cool and cloudy day.

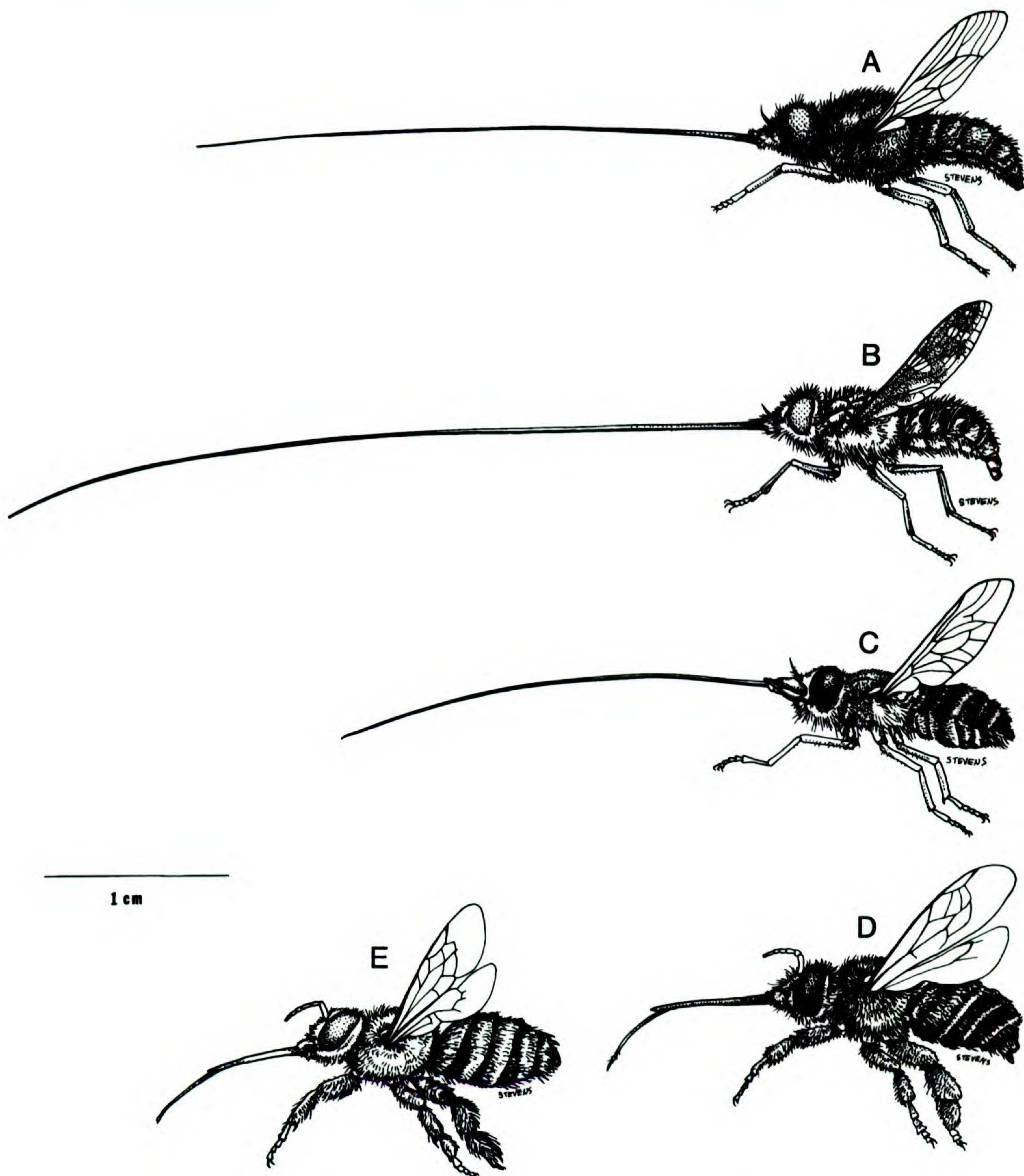


FIGURE 4. Primary pollinators of various species of subgenus *Lapeirousia*.—A. *Prosoeca peringueyi* (on *L. jacquini*).—B. *Moegistorhynchus longirostris* (on *L. anceps*).—C. *Philoliche gulosa* (on *L. fabricii*).—D. *Anthophora diversipes* (on *L. divaricata*).—E. *Parafidelia major* (on *L. barklyi*). Scale bar = 10 mm.

Philoliche gulosa visited *Lapeirousia fabricii* at three sites between 11 AM and 3 PM. The foraging behavior of *Moegistorhynchus longirostris* and *P. gulosa* on *Lapeirousia* species was similar to the foraging behavior of *Prosoeca* species. Nemestrinid species fly with their mouth parts hanging downward, and forage for nectar by extending the fairly flexible proboscis either forward or downward depending on the characteristics of a particular flow-

er. *Philoliche gulosa* flies with its proboscis extended forward, and its proboscis appears to be less flexible (S. Johnson, pers. comm.). *Moegistorhynchus longirostris* interrupted its foraging on *Lapeirousia* species to forage on the flowers of *Pelargonium* species, and species of two other Iridaceae, *Geissorhiza exscapa* (Thunb.) Goldblatt and *Babiana tubulosa* (Burm. f.) Ker-Gawl. We assume that *B. brachystachys* (Bak.) G. Lewis, *Ixia paniculata*

Delaroche, *Tritonia crispa* (L. f.) Ker-Gawl., *Geissorhiza confusa* Goldblatt, and *Gladiolus angustus* L. (all Iridaceae) also belong to this guild, because their flowers are similarly constructed and colored. *Moegistorhynchus* was also observed attempting to forage on the spurred but nectarless terrestrial orchid, *Disa draconis* (L. f.) Sw. The foraging of the fly on the orchid suggests another example of pollination by deceit, as the orchid produces creamy white flowers with narrow purple nectar guides, similar to floral presentation in *L. anceps*.

3. The *L. divaricata* group. Species in this group were visited by various combinations of Lepidoptera, bees, and bombyliid flies (Table 2). *Lapeirousia exilis* and *L. plicata* appear to be pollinated by a combination of bombyliid flies and Hymenoptera, including the native *Apis mellifera* (Apidae: Fig. 3C) and *Tetraloniella karooensis* (Anthophoridae). These insects were observed to contact anthers and stigmas while foraging, and pollen was brushed onto their bodies passively. All of the insects collected on flowers in this group have mouth parts shorter than *Philoliche gulosa* and the three taxa of nemestrinid flies (Table 5). Bees were active throughout most of the day, but were observed most frequently during the cooler periods before 11 AM or after 4 PM. The noctuid moth, *Heliothis armigera* (Fig. 3D), was observed in large numbers foraging on *L. divaricata* at two sites between 3:30 and 6 PM. Bombyliid flies, bees, *H. armigera*, and the butterfly, *Cynthia cardui* (Nymphalidae), did not usually forage by hovering. In zygomorphic flowers these insects always perched on the lower tepals before foraging for nectar.

The only insect observed to feed while hovering was the sphinx moth, *Hippotion celerio* (L.), which was seen but not captured in a population of *Lapeirousia pyramidalis* subsp. *pyramidalis* near de Wet (Worcester District). Pollen load analyses (Table 2) indicate that *H. armigera* and *Cynthia cardui* may be poor vectors of pollen compared to bees.

All bees collected on the *Lapeirousia divaricata* group belonged to long-tongued families. With the exception of two specimens of *Hoplitis similis* (Megachilidae) and one specimen of *Parafidelia* (Fideliidae), bees collected on the *L. divaricata* group belong in the families Anthophoridae and Apidae. Two anthophorid bee individuals collected (*Anthophora diversipes* and *Amegilla grisella*) were males, and the remainder, female. Analyses of pollen washes of the hairs on the hind legs and ventral abdominal region show two characteristics. First, all female bees collected on the *L. divaricata* group are polylectic and polytrophic. Field observations as well as pollen-load analyses showed that these

bees collected pollen actively on nectarless flowers including *Cyanella alba* L. f. (Tecophilaeaceae) and *Hermannia* sp. (Sterculiaceae). *Hoplitis similis*, collected on *L. spinosa*, interrupted its visits to this species to forage on similarly pigmented *Moraea tortilis* Goldblatt, the flower of which is also a meranthium of the gullet type "blossoms" (see below), similar to that of *Iris*. The flowers of *M. tortilis* produce small quantities of nectar. Pollen-load analyses showed that all bees foraged on a much broader selection of taxa than were recorded for fly or moth specimens. Although female bees do not collect pollen actively on *Lapeirousia* flowers, the pollen deposited passively on the bee's head and thorax is combed off by the bee and deposited in the scopae. Bee activity in species of the *L. divaricata* group differed during the season. *Apis mellifera* was collected most frequently in July and early August, while the first anthophorids were not observed and netted until mid August.

DISCUSSION

The limited published research on pollination ecology within the Iridaceae has tended to emphasize genera with meranthia of gullet flowers such as *Iris*, *Moraea*, and *Gynandriris* (Faegri & van der Pijl, 1979). The pollination ecology of *Lapeirousia*, however, is far closer to what has been described in the southern African genus *Nivenia* (Goldblatt & Bernhardt, 1990). In *Nivenia* floral tubes are not occluded and the stamens and styles are prominently displayed. The flowers are pollinated by long-tongued bees and nemestrinid flies in the genus *Prosoeca*. Access to the nectar-secreting tube is direct, and the insect head and thorax contact the anthers and stigma while the insect hovers or clings to the tepals.

The disparity between the length of the perianth tube in subgenus *Lapeirousia* and the shorter length of the mouth parts of the primary pollinators is quite easy to explain. Records of nectar secretion show that species in subgenus *Lapeirousia* secrete copious amounts of fluid for insect-pollinated flowers, and it is most unlikely that dominant pollinators are ever forced to extend their mouth parts to the base of the tube unless all the nectar has been removed by earlier foragers. More important, Darwin (1862) hypothesized that successful pollination of spurred orchids occurred when orchids evolved floral spurs slightly longer than the tongues of their pollinators, forcing the insect to ram its head down the floral throat, ensuring contact between the insect's head and the orchid's column. This has since been shown experimentally by Nilsson (1988). As

in the nectariferous orchids, species in subgenus *Lapeirousia* “oblige” their pollinators to make contact with the anthers and stigmatic surfaces of the style branches of the flowers that block or at least encircle the entrance to the floral tube.

Some members of subgenus *Lapeirousia* appear to be self-compatible. Spatial isolation between anthers and stigmas is not always well expressed in subgenus *Lapeirousia* and protandry is weakly developed. Four *Lapeirousia* species show successful fruit and seed production in the absence of pollinators. This is most likely the result of mechanical autogamy. (We consider the alternative possibility that apomixis takes place most unlikely: the phenomenon is unknown in Iridaceae.) Three of the four species that show self-pollination start flowering during the southern African winter, when rain and low temperatures may restrict pollinator activity. Mechanical autogamy by contact between the stigmatic surfaces and the pollen (or apomixis) then becomes a fail-safe mechanism in the absence of dependable pollinators. This has also been described in the late winter-early spring flowering herbs of North America (Schemske et al., 1978) and some terrestrial orchids of southern Australia (Dafni & Bernhardt, 1990).

There are two major differences between floral mechanisms in *Nivenia* versus *Lapeirousia*. First, fly pollination in *Nivenia* appears to be restricted to nemestrinids. In some *Lapeirousia* species pollination may be dependent on the long-tongued tabanid, *Philoliche gulosa*. Second, and more important, analysis of floral presentation and observation of floral foragers emphasize that pollination systems in southern African species of subgenus *Lapeirousia* can be subdivided into a minimum of three syndromes, or perhaps four if the sphinx moth syndrome is regarded as separate from the generalist system that otherwise prevails in those species with the *L. divaricata*-type flower.

Pollination by nectar-foraging flies has been treated as a relatively common but unspecialized syndrome in which many fly taxa visit the same flower, and the dispersal of pollen may be shared with co-foraging bees and butterflies (Grant & Grant, 1965; Barth, 1985). We may compare the more classical treatment of myophily with our results. Fly-pollination in *Lapeirousia* has evolved into such a specialized syndrome that two different modes of floral presentation appear to attract and depend on two different sets of fly genera. Species with the *L. silenoides*-type of flower appear to depend exclusively on two species of flies in one genus, *Prosoeca*. We also note that plants with the *L. silenoides*-type flower appear to be restricted to the

west coast and adjacent near interior of southern Africa. The species exhibiting the *L. fabricii*-type of presentation frequently have marginally longer tubes than species that have the *L. silenoides*-type flower and seem to be pollinated exclusively by *Moegistorhynchus longirostris* and *Philoliche gulosa*. Plant species with this flower type occur widely across southern Africa, although they appear to be most frequent in the southwest and west of the subcontinent. Among the species with this type of flower, *L. anceps* stands out in its remarkable range of perianth tube lengths, 20–76 mm. The pattern suggests that only populations in the west and north of its range with tubes 45–76 mm long are pollinated by *M. longirostris*, because nectar is accessible to only this fly, given the length of its proboscis. Populations with shorter tubes, as little as 20–30 mm in the south of its range, cannot be pollinated by this fly species, which does not occur in this part of the range of *L. anceps*. The pollinator(s) for these short-tubed plants must be some other, presumably long-tongued fly, possibly *Philoliche gulosa*, which does occur here and has a proboscis 20–33 mm long. Evidently, tube length is extremely labile and may respond rapidly to selection by pollinators.

Despite the segregation of *Lapeirousia* species into three pollination guilds, the majority of species in this subgenus secrete sucrose-rich/sucrose-dominant nectar regardless of the major pollinators. This adds a new dimension to the analytic work and categorization of nectar by Baker & Baker (1983, 1990). In their earlier treatments of myophily the Bakers found that fly-pollinated flowers tended to be weak in sucrose, like the flowers pollinated by short-tongued bees. However, when the Bakers analyzed fly flowers they concentrated on taxa pollinated by short-tongued flies, such as the Muscidae, Syrphidae, and Phoridae. It now appears that just as flowers pollinated by long-tongued bees are usually rich in sucrose (Baker & Baker, 1983, 1990), flowers pollinated by long-tongued flies are also sucrose producers. Perhaps pollination by large-bodied, physically active insects that maintain wing movement while feeding (e.g., nemestrinids, *Philoliche*, sphinx moths and some anthophorids (Goldblatt & Bernhardt, 1990)) requires an emphasis on sucrose instead of hexose rewards that is independent of insect order.

Although certain *Lapeirousia* species may be pollinated by only one or two fly species, the degree of dependency in this insect-flower relationship is not shared to the same degree by the flies. As in so many proposed cases of co-adaptation, the *Lapeirousia* flowers appear to have become modified for pollination by specific flies to a greater extent than

flies have become modified for *Lapeirousia* flowers. The evidence for this unequal relationship is presented in the polytrophic foraging behavior of flies at field sites and confirmed by the results of pollen load analyses. It is more likely that the *Lapeirousia* species with *L. silenoides*-type and *L. fabricii*-type flowers belong to broader guilds, encouraging the partitioning of long-tongued fly pollination into more than one syndrome in the southern African flora. Observations on flowers in other genera and families visited by long-tongued flies, e.g., *Babiana* and *Hesperantha* (Iridaceae), *Pelargonium* (Geraniaceae), suggest that floral presentation for pollination by *Prosoeca* species or by *Moegistorhynchus* and *Philoliche* shows a high degree of convergence in such floral characters as color patterns and tube or spur length. The types of floral presentation in southern African plants pollinated by different fly genera and species may ultimately prove to be as diverse as, yet distinct from, pollination guilds in other parts of the world, such as members of the neotropical flora that are pollinated by straight-billed hummingbirds versus those plant taxa pollinated by hermit hummingbirds with curved bills (Feinsinger & Colwell, 1978; Feinsinger et al., 1985).

Pollen-load analysis of the bee-pollinated members of the *Lapeirousia divaricata* group suggests community dynamics typical of flowers pollinated by long-tongued bees in other parts of the world. These anthophorids and long-tongued bees in the Apidae (e.g., *Bombus*, *Euglossa*) often show foraging strategies in which individual bees balance visits to nectarless flowers (e.g., *Dianella* (Phormiaceae), *Echeandia* (Anthericaceae), *Schrankia* (Fabaceae), *Acacia* (Fabaceae), *Hibbertia* (Dilleniaceae)) that offer copious pollen with visits to plants that produce copious nectar, but from which pollen is not collected actively (Bernhardt, 1989, 1990; Bernhardt & Montalvo, 1979; Bernhardt, 1995). The presence of the pollen of nectarless *Cyanella* and *Hermannia* on female anthophorids collected on flowers of the *L. divaricata*-type suggests that community pollination by long-tongued bees in southern Africa may not be significantly different from those syndromes cited above for the floras of Central America and southern Australia, and the woodlands and prairies of North America (Schemske et al., 1978).

Members of subgenus *Lapeirousia* now join an expanding list of plant taxa in which segregated pollen flow is due in part to ethological isolation (Grant, 1994). In subgenus *Lapeirousia* ethological isolation (sensu Grant, 1994) appears to be based on two factors. First, as in *Aquilegia* (Ranuncula-

ceae), different pollinators may be restricted to different plant taxa as a partial consequence of mechanical isolation (Grant, 1971), as bees and moths are probably unable to forage successfully on the flowers of *Lapeirousia* species in which tube length far exceeds tongue length. Second, ethological isolation must also be based in part on flower constancy as differing modes of floral presentation, featuring diverse color patterns and scent production, produce different responses in the foraging behavior of local pollinators that are polytrophic and/or polylectic. That is, flies and bees are not expected to respond to the same forms of floral advertisement due to their different visual and olfactory senses (Barth, 1985).

Observations of interspecific hybridization in sympatric and co-blooming populations of *Lapeirousia fabricii* and *L. jacquinii*, and of *L. silenoides* and *L. verecunda*, respectively, indicate that when members of the different pollination guilds are sympatric, ethological mechanisms are sometimes insufficient to prevent interspecific pollination, as evidenced by the recent discovery of scattered hybrids between members of each of the above pairs. In fact, species belonging to different guilds seldom co-occur, and when they do they usually flower at different times. These observations suggest that floral divergence is not a result of selection for prepollination isolating mechanisms.

Postpollination isolating mechanisms may operate in *Lapeirousia jacquinii* and *L. violacea*. These species belong to the same guild and have been seen to be visited by the same fly individuals. Despite this, no F1 hybrids have been found after three years of fieldwork, and it seems likely that biochemical recognition and rejection of interspecific pollens may be a more important form of interspecific isolation within some *Lapeirousia* species belonging to the same pollination guild. However, in other instances interspecific pollen recognition may offer incomplete isolation, as *L. jacquinii* and *L. pyramidalis* subsp. *regalis* have the same mode of floral presentation and hybrids between the two have been recorded at one site (Goldblatt & Manning, unpublished).

Information on pollination systems in subgenus *Lapeirousia* may now be combined with a cladistic analysis to help determine the evolution of pollination syndromes, extensively discussed by Goldblatt & Manning (in mss.). The picture that emerges from that study (Fig. 5) indicates most strongly that the dependence of a *Lapeirousia* species on a particular guild of long-tongued pollinators has originated several times. While it is true that some sister species (e.g., *L. dolomitica* and *L. violacea* or *L.*

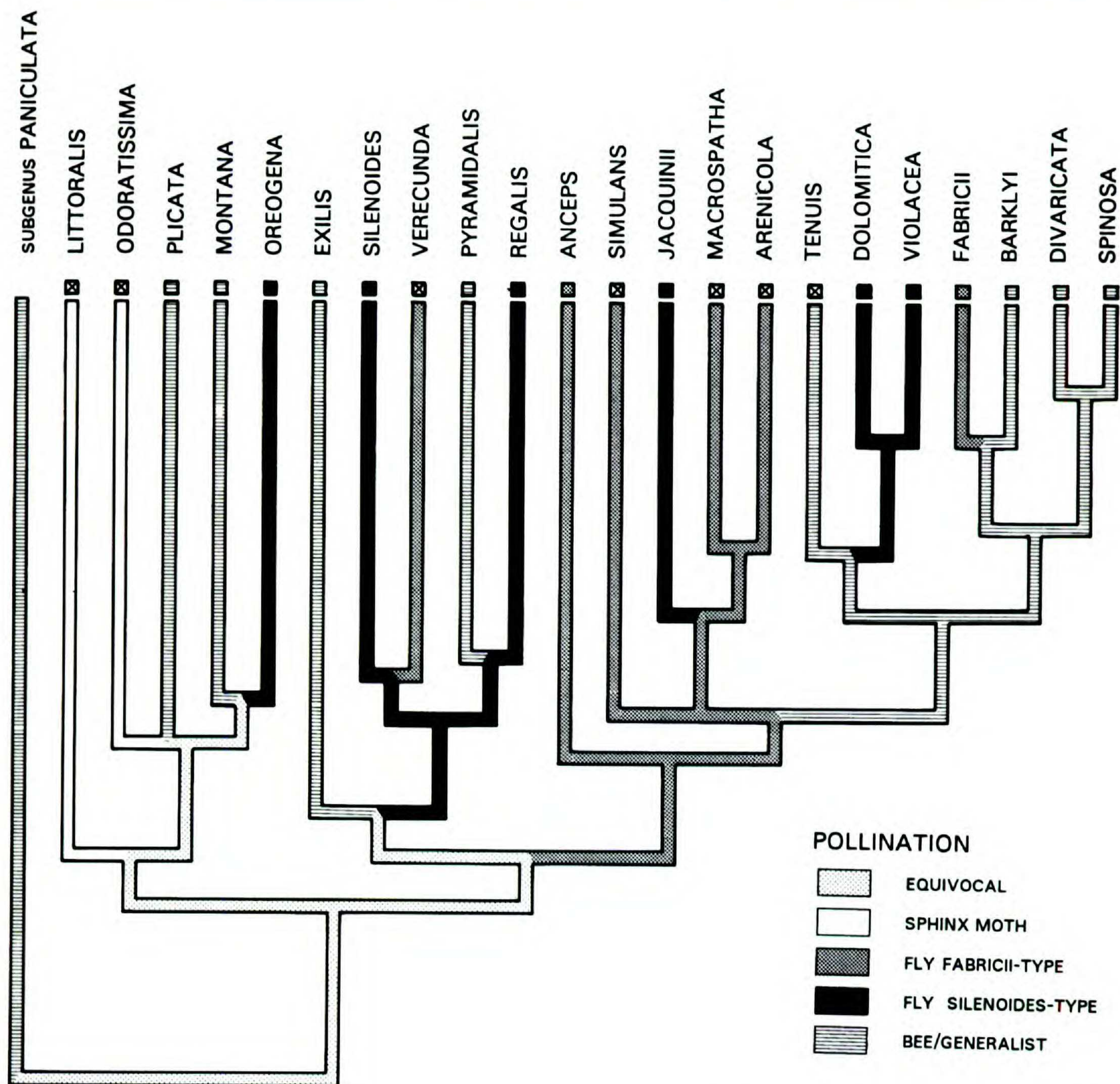


FIGURE 5. Phylogenetic tree showing putative relationships of the species of subgenus *Lapeirousia* (from Goldblatt & Manning, in mss.) with pollination syndromes mapped on the branches. The cross in the block below the species name indicates pollinator(s) inferred from floral morphology. The tree is one of four equally parsimonious trees obtained using the Hennig86 package of programs for cladistic analysis (Farris, 1988), after successive weighting, consensus index (C.I.) 81, retention index (R.I.) 91. The initial analysis using the mh* and bb* options yielded 1332 equally parsimonious trees, length 74, C.I. 48, R.I. 67. The four final trees differed in the position of only two terminal taxa and do not affect our conclusion that the two long-tongued fly pollination systems evolved independently several times in subgenus *Lapeirousia*. The details of the cladistic analysis are presented in detail in a separate paper (Goldblatt & Manning, in mss.).

divaricata and *L. spinosa*) share the same pollination syndrome, this sharing appears to be an exception within the current phylogenetic tree. From the combined data we conclude that floral evolution in subgenus *Lapeirousia* is extremely labile and probably reflects a rapid response to the relative diversity of potential vectors within a given geographic area.

It is possible to predict with some degree of con-

fidence the ancestral mode of pollination within subgenus *Lapeirousia*. We know that in the out-group, subgenus *Paniculata*, the majority of species bear relatively short-tubed flowers with pollination types most similar to the *L. divaricata*-type in subgenus *Lapeirousia*. Goldblatt (1990) reported that two species, *L. erythrantha* (Klatt) Bak. and *L. avasmontana* Dinter (both tropical members of subgenus *Paniculata*), are actively visited by bees,

wasps, and diurnal Lepidoptera, and *L. sandersonii* Bak. of the subgenus is visited predominantly by diurnal Lepidoptera (Manning, unpublished). This is consistent with our observations here (Table 2) for *L. azurea* (Eckl. ex Bak.) Goldblatt, *L. fastigiata* (Lam.) Ker-Gawl., and *L. neglecta* Goldblatt & Manning, and Scott Elliot's (1891) report for *L. corymbosa* (all subgenus *Paniculata*), also most commonly visited by bees. Therefore, short-tubed and funnel-shaped flowers dependent on Hymenoptera and Lepidoptera may be basal to subgenus *Lapeirousia*, and it seems far more parsimonious to infer that flowers with long perianth tubes and associated nectar guides are ultimately derived from short-tubed flowers with simple nectar guides. In light of this, the terminal position of the species pair, *L. divaricata*-*L. spinosa*, primarily pollinated by bees, and nested within a clade of long-tongued fly-pollinated taxa, evidently represents a reversal to an ancestral pollination strategy. This emphasizes the extreme degree of adaptive radiation exhibited within subgenus *Lapeirousia* and the impact of pollinators on floral morphology and biochemistry.

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